Trees

Direct Penman-Monteith parameterizations for estimating stomatal conductance and modeling sap flow

--Manuscript Draft--

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Abstract:	The Penman-Monteith equation of evaporation is often combined with sap flow measurements to describe canopy transpiration and stomatal conductance. The traditional approach involves a two-step calculation. In the first step, stomatal conductance is computed using an inverted form of Penman-Monteith equation. The second step correlates these values with environmental factors. In this work, we present an improved approach for direct parameterization of the Penman-Monteith equation developed to compute diurnal courses of stand canopy conductance (gc) from sap flow. The main advantages of this proposed approach versus using the classical approach are: (1) the calculation process is faster and involves fewer steps, (2) parameterization provides realistic values of canopy conductance, including conditions of low atmospheric vapor pressure deficit (D) whereas the traditional approach tends to yield unrealistic values for low D and (3) the new calculation method does not require enveloping curves to describe dependence of gc on D and thus avoids subjective data selection but it still allows to visualize separable responses of gc to environmental drivers (i.e. global radiation and vapor pressure deficit). The proposed approach was tested to calculate gc and to model the sap flow of a high mountain Pinus canariensis forest. The new calculation method permitted us to describe the stand canopy conductance and stand sap flow in sub-hour resolution for both day and night conditions. Direct parameterization of the Penman-Monteith approach as implemented in this study proved sufficiently sensitive for detecting diurnal variation in gc and for predicting sap flow from environmental variables under various atmospheric

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	evapotranspirative demands and differing levels of soil water availability.
Response to Reviewers:	Ulrich E. Luettge Editor-in-Chief Trees - Structure and Function Dear Prof. Dr. Luettge First of all we sincerely thank you for your editorial decision and for the useful comments and helpful suggestions of the reviewers. We now have considered and incorporated the reviewers' comments and suggestions in the revised text. Please find below our answers to the reviewers' specific comments. We are convinced that the revised manuscript has been significantly improved and will now be acceptable for publication in your Trees - Structure and Function. Yours sincerely Josef Urban, on behalf of the co-authors Answers to the reviewers' specific comments: Reviewer #3: Authors' response: As suggested, we enlarged the introduction and the discussion sections. We explained the reasons for using the Jarvis and Lohammar models instead of the Ball Berry model. We much appreciate Ball Berry model (and its future modifications) and its use in the global circulation models and in the models which include net photosynthesis. We are aware of the limitations of the Lohammar and Jarvis-Stewart models that we use, and that is also why we proposed to include the parameter of minimal stomatal conductance, similar to the one used by the Ball Berry model. Comparing to the Lohammar model, the inclusion of net assimilation (and its correlation with the stomatal conductance) into the Ball Berry model reduced the number of free parameters, which is definitely a great advantage. On the other hand, when using the Ball Berry model, the net assimilation has to be either measured or simulated by the biochemical models. Many of the sap flow studies do not have data on photosynthesis available (even though the already published values from the similar sites or tree species can be used too). Also, unlike the sap flow, photosynthesis cannot be easily measured on the whole tree level which also brings along the scaling issues. Therefore the Jarvis-Stewart and Lohammar models are still used in the simple studies like ours for they simplicity, when the burden of measuring and modeling of photosynthesis does not justify the advantages of its inclusion. Moreover, the Ball Berry model has some limitations too. Even though the fixed relationship between the assimilation and stomatal conductance holds for the most of the situation, it changes sometimes One example may be the drought (which occurred in our study and also in the study of Xu, Medvigy et al. (2016), where at Fig. 4a the sap flow almost do not change in the daytime between dry and wet season while the net assimilation decreases: maybe among others due to the changes in mesophyll conductance which affect the CO2 transfer to the chloroplasts and do not such have effect on water vaporization) and the other example the extreme temperatures during heatwaves. We agree that there is a large array of the models which provide more mechanistic insight to the stomatal functioning then ours, among them the works of Xu, Medvigy et al. (2016) and Mirfenderesgi, Bohrer et al. (2016). On the other hand, there are even more detailed models of stomatal behavior, which include processes on the membranes of guard cells. All of them have their place in the tree research and none of them is ideal for all kind of applications. There are still papers being published which use the methodology we try to improve and that's why we think we have reason to care about this kind of models too. We included some more references of papers using approach similar to ours to highlight relevance of our study. Reviewers' question: What is the physical rationale behind the use of the arctangent function in equation 4? Authors' response: Some data suggested, that stomata response to D may not be always exponential and that stomata may slow down its opening at low vapor pressure deficit (i.e. Jones 2014, p. 140, Fig. 6.10, Bourne et al. 2015, Fig. 2), we introduced an arc tangential relationship allowing for more precise descriptions of stomata behavior at low D. Because gasometrical measurement suffer difficulties at large air humidities due to the condensations, there are not many data available and the proposed arctangential function may not be the best one. On the other hand, it yielded the highest R2 and lowest AIC which suggest that its use may be rational. Reviewers' question: The methodology of Ewers, Mackay et al. (2007) for estimating

stomatal conductance on the basis of observed sap flow does suffer from difficulties at low VPD, but in what scenarios would it be beneficial to back calculate sap flow and stomatal conductance from the PM model when neither are observed?
Authors' response: The analysis allows describing the response of gc of the particular tree species to various environmental drivers (i.e. Rg or D). Sap flow calculated by this method may also be used for simulation of water use of the forests when it was not measured or to fill the gaps in the sap flow measurements.
Reviewers' question: Importantly, why would one chose to use this method to back calculate sap flow, over a mechanistic model that represents physical pathway of the soil-plant-atmosphere continuum as is becoming increasingly common using the models the authors cite in line 360 as well in the works of Xu, Medvigy et al. (2016) and Mirfenderesgi, Bohrer et al. (2016)?
Authors' response: There is a large array of the models to describe the tree water relations. Our method (in its 'classical' approach) is quite commonly used due to its simplicity and ability to describe separate responses of stomatal conductance to various environmental drivers. One advantage of this simple approach is that that almost everyone is able to calculate stomatal conductance. The other point is that in such a simple model there are not many parameters to be mutually adjusted. I admire the accuracy with which can the FETCH2 model predict the forest transpiration. On the other hand there may arise the questions about how accurately are the underlying processes described. For example in the work of Mirfenderesgi et al. (2016), Fig. 1b: is really the P50, the point where the 50 % of the xylem conductance is lost, in a pine as low as about the -1MPa? Or is it just a result of numerical solving and mutual adjustment of many parameters? Is the pine more vulnerable to cavitation than oak? How does it match to the published data? This is the point where the complex models can provide questions about plant and ecosystem functioning but we should be careful about taking the model results as answers.
Reviewers' question: L62-64: How can stomatal conductance be dependent on soil moisture and xylem architecture while excluding controls imposed through the actual xylem/tracheid pathway? I.e. soil moisture governs root water availability, which governs root water potential, which acts with xylem architecture to govern xylem water potential, which in turn governs leaf water potential which influences stomatal conductance.
Authors' response: We improved the wording at this point of the manuscript: L58 - 63
Reviewers' question: L68: Also importantly (Collatz, Ball et al. 1991) and (Ball, Woodrow et al. 1987)
Authors' response: We added these references to the text.
Reviewers' question: L88: Subject verb agreement 'substitutes'
Authors' response: Changed as suggested.
Reviewers' question: L89: The subject of this sentence is missing
Authors' response: The subject of the sentence was added.
Reviewers' question: L112: What is the site's typical VPD range since we are talking about why it is important not to have to discard data when VPD is low? What fraction of half hours would have to be discarded during a typical growing season because VPD is below 600kPa?
Authors' response: We included reference to the Fig. 2 and added the exat number of rejected values (818 out of the measured 1872 values) on the L255.
Reviewers' question: L140-Forward: This would be clearer if it were presented in a table for all variables used throughout the paper.
Authors' response: We created a table with abbreviations as suggested.
Reviewers' question: L170: What is the specific justification for the arctan term? How was this developed/determined?
Authors' response: We answered to this question in one of the previous questions of this letter and also added the explanation to the manuscript.
Reviewers' question: L174: Should be gmax?
Authors' response: Glim is the theoretical maximum of the arctangential function which may be higher than maximum gs observed at zero D. Therefore we prefer to use the term glim.
Reviewers' question: L213-217: What were the soil water potential ranges during each period?
Authors' response: We added the SWP to the lines 215-222
Reviewers' question: L226: On what time scale, specifically?
Authors' response: We changed the wording to: 'These calculations were performed in 24 hour resolution within a period from 15 February to 1 September, 2008.'

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Reviewers' question: L227-230 This makes no sense. Why would you parameterize a model for something only to change your parameters specifically when the model did not fit?
Authors' response: We tried to better explain as: 'In a two-week long period from 25 May to 10 June, following a rainfall event, gypsum block sensors indicated an increase in soil water potential which, however, was not entirely reflected in tree sap flow (Figs. 2b and 3). This prompted us to use linear interpolation for the SWP between the beginning and end of this period, from 25 May to 12 June and to use only these data for the model parameterization.'
Reviewers' question: L234-238: Did any or none of these include the effect of soil water potential?
Authors' response: None of them included the effect of SWP, we added this information on the lines 250-251.
Reviewers' question: L241-2: Were they not compared directly to field measurements of sap flow?
Authors' response: We improved the wording here: 'Values of modeled sap flow and canopy conductance were compared to the sap flow measured in the field and to a canopy conductance calculated from an inverted P-M equation (7).'
Reviewers' question: L247: True, but isn't your whole argument that your methodology is superior than the classic method particularly in cases of low D? In that case, why continue to not simulate times when D is low? Wouldn't the authors want to make the comparison during these times in particular?
Authors' response: We did two comparisons: First one for the period where classical approach work without problems to prove that proposed approach provide comparable results. Second comparison included also the period where classic method fails, to demonstrate that proposed method works even during this period. We also improved the text of the manuscript here.
Reviewers' question: L261: differences?
Authors' response: Changed as suggested
Reviewers' question: L264: discrepancies?
Authors' response: Changed as suggested.
Reviewers' question: L270: Most other stomatal conductance models include a gmin parameter (typically, go) which, again, raises the question why the authors chose to use the Lohammar model rather than a more broadly used and accepted model for stomatal conductance?
Authors' response: We believe that we explained the reasons at the beginning of this letter as well as in the introduction section of the manuscript.
Reviewers' question: L294: If this is the case, again, why not use a more broadly accepted gs model that already includes a go term??
Authors' response: We believe that we explained the reasons at the beginning of this letter as well as in the introduction section of the manuscript.
Reviewers' question: L357-9: All of these models are for porous media flow. Could you provide examples of R-C models as well?
Authors' response: We added those models as suggested.
Reviewers' question: L360: The work of Matheny, Bohrer et al. (2015) and Oliva Carrasco, Bucci et al. (2015) have developed new measurement technologies for measuring water content directly in the stems of large trees at time steps smaller than a half hour.
Authors' response: We added these references and a one to the previous work on this topic to the text: L381-383.
Reviewers' question: L360-362: None of the models cited in L358 require the measurement of water potential to run or even to evaluate. All models solely require sap flux to parameterize the model in order to solve for water potentials, from which stomatal conductance is calculated.
Authors' response: We added a sentence of discussion on this topic on lines 376-379.
Reviewers' question: L390-1: Why is this not discussed in the results section?
Authors' response: We added these results to the lines 314-317.
Reviewers' question: Fig2: Soil water potential remained 100% constant from July through September?
Authors' response: -1.1 MPa was the limit of the equipment. This information is now on the lines L154 and 222.
Reviewers' question: Fig3: What do you mean by "modeled from wet period"? Is this using parameters that were established specifically for times during wet soils? Why is it more practical to re-parameterize a model in the middle of the growing season rather

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	than to include a more accurate representation of the dynamics that limit water availability? Authors' response: We improved the figure caption. The explanation for the reason for modeling of the sap flow using the parameters from the period of unlimited water availability was included to the lines 271-272

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Direct Penman-Monteith parameterizations for estimating stomatal conductance and modeling sap flow

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Abstract

The Penman-Monteith equation of evaporation is often combined with sap flow measurements to describe canopy transpiration and stomatal conductance. The traditional approach involves a two-step calculation. In the first step, stomatal conductance is computed using an inverted form of Penman-Monteith equation. The second step correlates these values with environmental factors. In this work, we present an improved approach for direct parameterization of the Penman-Monteith equation developed to compute diurnal courses of stand canopy conductance (g_c) from sap flow. The main advantages of this proposed approach versus using the classical approach are: (1) the calculation process is faster and involves fewer steps, (2) parameterization provides realistic values of canopy conductance, including conditions of low atmospheric vapor pressure deficit (D) whereas the traditional approach tends to yield unrealistic values for low D and (3) the new calculation method does not require enveloping curves to describe dependence of g_c on D and thus avoids subjective data selection but it still allows to visualize separable responses of g_c to environmental drivers (i.e. global radiation and vapor pressure deficit). The proposed approach was tested to calculate g_c and to model the sap flow of a high mountain *Pinus canariensis* forest. The new calculation method permitted us to describe the stand canopy conductance and stand sap flow in sub-hour resolution for both day and night conditions. Direct parameterization of the Penman-Monteith approach as implemented in this study proved sufficiently sensitive for detecting diurnal variation in g_c and for predicting sap flow from environmental variables

under various atmospheric evapotranspirative demands and differing levels of soil water availability.

Keywords: canopy conductance; transpiration; trunk heat balance; Penman-Monteith; alpine forest.

Key message: The novel approach for direct parameterization of the Penman-Monteith equation was developed to compute diurnal courses of stand canopy conductance from sap flow.

1. Introduction

In the average, transpiration accounts for 61 % of the evapotranspiration (Schlesinger and Jasechko 2014). It means, that most of water evaporated from the ecosystems has to pass through the plant and that its precise amount is regulated by the vegetation. Therefore, the evaporation models have developed from the purely physical approach (i.e. Penman 1948) to the ones that implemented the principles of turbulent diffusion theory and plant stomatal regulation (Monteith 1965). In coniferous and other stands, with strong coupling between the canopy and the atmosphere, g_c (see Table 1 for the list of abbreviations) has a major effect on transpiration (Jarvis and McNaughton 1986; Meinzer et al. 1997; Phillips and Oren 1998; Hernandez-Santana et al. 2016). If evapotranspiration can be measured, actual stomatal conductance can then be easily calculated by using an inverted Penman-Monteith equation (Martin et al. 1997; Cienciala et al. 1997; Granier et al. 2007; Whitley et al. 2009; Braun et al. 2010; Wang et al. 2014; Fu et al. 2016). This equation combined with sap flow measurements provides a powerful tool for estimating canopy conductance for both whole-tree and forest stand levels with results comparable to leaf level measurements with subsequent upscaling (Ewers et al. 2007b).

The aim of calculating stomatal conductance with the P-M equation is to determine to what extent g_c is dependent on environmental variables such as solar radiation and air vapor pressure deficit (Lohammar et al. 1980; Oguntunde et al. 2007), which may be combined for example with air temperature (Jarvis 1976; Stewart 1988; Sommer et al. 2002), soil moisture (Stewart 1988; Granier and Loustau 1994; Harris et al. 2004), and eventually xylem architecture (Zhang et al. 2011). A range of functions exist for these models, from a simple linear approach (Oguntunde et al. 2007) using more complicated non-linear equations relating two (Lohammar et al. 1980) or more (Jarvis 1976) environmental variables, to

complex models incorporating photosynthetic and biochemical regulation to measure stomatal conductance (Ball et al. 1987; Collatz et al. 1991; Tardieu and Davies 1993; Leuning et al. 1995; Jarvis and Davies 1998; Berry et al. 2010; Buckley et al. 2012; Mirfenderesgi et al. 2016; Xu et al. 2016). However, parameterizing the lastly mentioned models which include photosynthesis has become increasingly difficult due to varying degrees of model sophistication and limited data availability for most field studies (Ward et al., 2008). For this reason, empirical models are commonly selected to focus on two primary environmental drivers: R_g and D. In conditions of limited soil water content, soil water deficit may be added as a third driver.

There are two main types of the empirical (phenomenological) models of the stomatal conductance. First group is represented by the Jarvis-Stewart (Stewart 1988) and the Lohammar model (Lohammar et al. 1980). These models predict stomatal responses solely on the base of environmental factors. This approach is still widely used because it is simple and its modular structure makes it easy to incorporate in the larger models, and because its responses to the environmental factors can be separated and visualized (Egea et al. 2011; Buckley and Mott 2013). For its simplicity this kinds of models are also used to derive stomatal conductances from the sap flow measurements (Lu et al. 1995; Cienciala et al. 1997; Whitehead 1998; Oren et al. 1999; Ewers and Oren 2000; Ewers et al. 2007a; García-Santos et al. 2009; Wang et al. 2014; Fu et al. 2016). In such a cases, the simple models are often preferred over the more recent Ball-Berry model and its modifications, which are otherwise widely used in canopy and global circulation models (Verhoef and Egea 2014). The main complication for the use of Ball-Berry model in derivation of g_c from the sap flow is that it requires the knowledge of net assimilation. Net assimilation can be directly measured (which data are not always available with sap flow measurements) and then plotted against measured g_s or modeled from biochemistry of photosynthesis but it presents an extra effort that does not need to be done when using the simpler Lohammar model. For the sake of simplicity and to make our work comparable to similar studies (i.e. Oren et al. 1999; Ewers and Oren 2000; Ewers et al. 2007a; García-Santos et al. 2009; Wang et al. 2014; Fu et al. 2016) we decided to use those kinds of empirical models that do not include the photosynthesis.

In the classical process for deriving stomatal conductance from sap flow measurements, g_c is calculated using the inverted form of the P-M equation followed by regression analyses usually performed between individual environmental variables and g_s. One disadvantage of this approach is that it requires using an enveloping curve for D and excluding data when D rates are low to avoid unrealistically high values of g_s (Phillips and Oren 1998; Ewers and

Oren 2000; García-Santos et al. 2009). This paper proposes an improved way of modeling canopy sap flow in a forest stand through direct parameterization of a P-M equation. Above mentioned traditional approach first (i) calculates the g_c from inverted P-M equation, than (ii) it rejects all data where g_c seem unrealistic (especially at low D), (iii) it searches for dependence between g_c and weather conditions using regression analysis and suitable (i.e. Jarvis-Stewart of Lohammar) model, (iv) substitutes that sub-model into the P-M equation and calculates the sap flow. In contrast, proposed approach enables to perform modeling of sap flow in one step and it does not require data rejection when D levels are low. The g_c and stomatal response to R_g and D can be computed in a second step from the Lohammar equation. We also propose a few modifications to the Lohammar equation. Because some data suggested, that stomata response to D may not be always exponential (i.e. Jones 2014, p. 140, Fig. 6.10, Bourne et al. 2015, Fig. 2), we introduced an arc tangential relationship allowing for more precise descriptions of stomata behavior at low D. An additional parameter describing minimal stomatal conductance (similarly to the parameters of 'b' or 'g_0' in Ball-Berry model and its modifications) was then introduced permitting calculation of nocturnal sap flow. The aim of this study is to improve how sap flow and stomatal conductance are modelled from Penman-Monteith equation, to test the applicability of proposed approach for modeling sap flow in a forest stand and to compare the results with those derived from using the more traditional approach. The analysis allows describing the response of g_c of the particular tree species to various environmental drivers (i.e. R_g or D). Sap flow calculated by this method may also be used for simulation of water use of the forests when it was not measured or to fill the gaps in the sap flow measurements.

2. Material and methods

2.1. Site description

The study was conducted in an open *P. canariensis* forest at its upper distribution limit at 2,070 m a.s.l. in the Teide National Park (28°18'21.5"N, 16°34'5.8"W), Tenerife, Canary Islands, Spain. At the time of the study (2008), the trees were 50–60 years old with a mean canopy height of 10.3 m. The stand density was 291 trees ha^{-1}, with a basal area of 16.7 m^2 ha^{-1}. The diameter at breast height (DBH) averaged 25.4 ± 9.3 cm (Fig. 1), and the plant area index (LAI) was 3.6 (Brito et al. 2014). The field site is characterized by a Mediterranean climate with alternating warm and dry periods from June to September, and a cold and wet period from October to May. During the period 1971–1999, mean annual precipitation recorded at the Portillo weather station located approximately 300 m southeast

of the study site was 368 mm, falling mostly during the winter months (December–February; 190 mm), while summer was the driest season (June–August; 3 mm). The mean annual air temperature was 10.7 °C. Daily means of global radiation, vapor pressure deficit, soil water potential and daily sums of precipitation within the investigated period are at the Fig. 2. The geologic substrate is of volcanic origin, and the soil at the study site is classified as a leptosol.

2.2. Field measurements

Sap flow was measured from 25 January to 10 September 2008. Ten sample trees with diameter at breast height (DBH) from 21 to 44 cm were selected for continuous sap flow measurements. Tree sap flow was measured by the tissue heat balance method with constant heating power (Čermák et al. 1973; Kučera et al. 1977) manufactured by EMS Brno, Czech Republic (type P4.1, heating power 0.63 W). Electrode lengths of 70 and 80 mm were used to cover the conductive sapwood depth. Thirty-minute averages from sap flow values measured in one minute intervals were stored on a data logger. Scaling up of sap flow from the sample trees to the stand level was based on the DBH of the sample trees and diameter distribution of the trees in the forest stand (Čermák et al. 2004), as well as for the study site, described in detail by Brito et al. (2014).

Environmental variables such as global radiation, air temperature, air humidity, precipitation and wind speed were taken from a meteorological station (uEMSet 99 (EMS Brno)) installed on an open plot close to the study site. Soil water potential between 0 and -1.1 MPa, which was the limit of the equipment, was measured with three gypsum blocks at depths of 25-30 cm (sensors GB2, Delmhorst, Inc., USA; datalogger ModuLog 1029, EMS Brno, Czech Republic). All environmental data were recorded with a 30-minute resolution.

2.3. Data processing

2.3.1. New approach: derivation of canopy conductance by direct parameterization of the Penman-Monteith equation

The analysis of canopy transpiration (E_p, mm h^{-1}) was made based on the P-M equation with the simplification that for long periods, stand transpiration equals sap flow. The general form of the P-M equation is:

$$\lambda E_p = \frac{\Delta\left(R_n - G\right) + \rho c_p D g_a}{\Delta + \gamma\left(1 + {}^{g_a}\!/_{g_c}\right)} \quad (1)$$

and the aerodynamic conductance is:

$$g_a = \frac{k^2 u}{\ln^2\left[\left(z-z_d\right)/z_0\right]} \quad (2)$$

All above listed variables were directly measured or calculated. The only unknown variable was canopy conductance g_c.

Parameterization of the P-M equation is based on the assumption that canopy conductance g_c depends on solar radiation and D, according to a suitable formula. We used a modified version of the Lohammar equation (Lohammar et al. 1980). The original form of this equation supposes that stomatal opening is caused by solar radiation and that stomatal closure results from high evaporative demands. Consequently, this proposes that stomatal closure is complete at night. However, calculating transpiration response to night D values called for an additional parameter (g_{min}), similarly as in the Ball-Berry model (Ball et al. 1987). Some measured data suggested, that opening of stomata in response to the D may not always follow strictly exponential manner (i.e. Jones 2014, p. 140, Fig. 6.10, Bourne et al. 2015). Therefore, alongside with the exponential form of the model, we also applied arctangent equation which gave us more flexibility when describing stomatal behavior under conditions of low D. The original form of the Lohammar model was:

$$g_c = \frac{R_g}{R_g + R_0} \cdot \frac{g_{max}}{1 + a.D} \quad (3)$$

and the proposed modification is:

$$g_c = g_{min} + \frac{R_g}{R_g + R_0} \cdot g_{lim} \cdot (0.5 - \frac{1}{\pi} arctg(\frac{D}{a} - b)) \quad (4)$$

The resulting form of the modified Penman-Monteith equation used for the parameterization was:

$$E = \frac{\left(\Delta.\left(R_n - G\right) + \rho c_p D g_a\right)/\lambda}{\Delta + \gamma.(1 + \frac{g_a}{g_{min} + \frac{R_g + 1}{R_g + R_o} \cdot g_{lim}(0.5 - \frac{1}{\pi} arctg(\frac{D}{a} - b))})} \quad (5)$$

The parameters a, b, R_0, g_{min} and g_{lim} were optimized by minimizing the residual sum of squares of the observed and modeled conductances. Calculations were performed using non-linear multivariate analysis with Mini32 statistical software (EMS Brno, Czech Republic).

Stomatal conductance (g_s) may be derived from canopy conductance (g_c) using the following equation:

$$g_c = g_s * LAI \quad (6)$$

The time lag between R_g, D (which determine foliar transpiration) and stem sap flow were estimated performing time series cross-correlation analysis. The respective environmental variable was shifted in thirty-minute step intervals and correlated to sap flow until the highest R^2 was reached. Only the lagged environmental data were used for parameterization of the P-M equation.

2.3.2. Classical approach

Results of the new approach were compared to a classically used method (Granier and Loustau, 1994). Here, the canopy conductance was calculated from the inverted form of the Penman-Monteith equation:

$$\frac{1}{g_c} = \left[\frac{s}{\gamma} \left(\frac{R_g - \lambda E}{\lambda E} \right) - 1 \right] \frac{1}{g_a} + \frac{\rho_a c_p}{E \lambda \gamma} D \quad (7)$$

Subsequently, canopy conductance was modeled using both a modified Jarvis-Stewart approach (Jarvis, 1976; Granier and Loustau, 1994) and a modified Lohammar model (eq. 4) which was previously used for the direct parameterization of the P-M equation. The Jarvis-Stewart model was used in the form:

$$g_s = a \left(\frac{R_g}{R_g + b} \right) \left(\frac{1 - cD}{1 + dD} \right) + g_{\min} \quad (8)$$

where *a, b, c, d* and g_{min} are estimated parameters based on the standard minimal sum of squares criterion. Modeled canopy conductance was used for modeling the canopy sap flow by applying the P-M approach. For parameterizations of equations 4 and 8 and classical approach we used data when D was higher than 600 Pa (Ewers and Oren 2000). These parameters estimated for high D were also use to model sap flow when the D was low.

2.3.3. Effect of soil water availability on sap flow

Three time periods characterized by contrasting soil water availability were apparent in the study period. The first, characterized by non-limiting water availability ('wet' period; mean soil water potential (SWP) was -0.02 MPa and it was always higher than -0.05 MPa within this period), lasted from the beginning of the year to the end of April. The second, the transient period, lasted from May to the middle of June. The SWP ranged between -0.05 and -1.1 MPa most of the time. The last, dry period, occurred from the middle of June until the

end of the investigated period. The SWP in this period was lower than -1.1 MPa, which was the lowest value that could be measured by the used equipment (Fig. 2). To avoid any adverse effects of soil water availability on the stand transpiration, initial parameterization of the proposed model was carried out for the period of non-limiting water access, from 27 February to 5 April, 2008. All comparisons between the proposed and classical approaches were drawn from this same period.

We later modified eq. 4 in a way that enabled us to use the soil water potential data to describe the effects of soil water availability on stomatal conductance:

$$g_c = g_{\min} + \frac{R_g}{R_g + R_0} \cdot g_{\lim} \cdot (0.5 - \frac{1}{\pi} arctg(\frac{D}{a} - b)).(c.\ln(SWP) + d) \qquad (9)$$

wherein *SWP* (MPa) represents the absolute value of soil water potential and *c*, *d* are parameter estimates. These calculations were performed in 24 hour resolution within a period from 15 February to 1 September, 2008. In a two-week long period from 25 May to 10 June, following a rainfall event, gypsum block sensors indicated an increase in soil water potential which, however, was not entirely reflected in tree sap flow (Figs. 2b and 3). This prompted us to use linear interpolation for the SWP between the beginning and end of this period, from 25 May to 12 June and to use only these data for the model parameterization.

2.3.4. Comparison among the sub-models for dependence of stomatal conductance on environmental variables and between classical and proposed approach

Three kinds of models for canopy conductance dependence on environmental variables (such as R_g, D) were applied during the process of direct parameterization. The Jarvis-Stewart model (8), both the original and the modified Lohammar equation (3, 4), and the three with the applied (or not applied) added parameter of minimal canopy conductance (g_{min}) – altogether provided six variants. These equations were included in the process of direct parameterization of the P-M equation to calculate sap flow and canopy conductance. Also, all these sub-models were used to calculate sap flow and g_c by classical approach. Values of modeled sap flow and canopy conductance were compared to the sap flow measured in the field and to a canopy conductance calculated from an inverted P-M equation (7). All simulations intended for the comparison among the models were performed for the period of non-limiting water access, from 27 February to 5 April, 2008 and therefore no submodel for the soil water potential was applied. It is well known that the occurrence of low D (high air humidity) leads to unrealistically high values of g_c calculated by the classical approach. For this reason Ewers and Oren (2000) recommended to remove all data where

the D is lower than 600 Pa from the analysis. However, in our case this would mean rejection of 818 out of the measured 1872 values. Therefore, we did two comparisons on two different datasets. First one covered entire wet period and included all data, including those when the D was lower than 600 Pa. The second dataset contained only 20 full days when the D was higher than 600 Pa.

3. Results

3.1. Measured sap flow

Daily maximum levels of sap flow for individual sample trees were between 10 to 67 kg day^{-1} with maximal values of stand sap flow 0.89 mm day^{-1} (Figure 3). Sap flow lagged behind evapotranspiration demands of atmosphere, R_g and D. Estimated time lags between the sap flow and climate variables were 60 minutes for R_g and 30 minutes for D.

3.2. Modeling sap flow and stomatal conductance: direct parameterization

Our proposed model successfully predicted diurnal courses of stand sap flow during the wet period, yielding $R^2 = 0.96$ and having the lowest AIC (Table 2), as soil moisture is not a limiting factor during this part of the season. However, the model parameterization for the wet season overestimated daily sums of sap flow during the transient and dry periods, beginning in May (Fig. 3). Differences between measured and modeled sap flow may be perceived as quantitative indicator of water deficit for the transpiration. The model provided an acceptable description of tree sap flow on a diurnal basis (Figs. 4, 5), and even took into account night flows. Discrepancies between measured and modeled values appeared after rainfall, when it was apparent that the sap flow based model could not accurately predict evaporation of intercepted water.

Parameterization of the P-M equation was further complicated by the occurrence of night sap flow. The Lohammar equation, in its original form (3), accounts for the full closure of the stomata and no cuticular transpiration, therefore for zero transpiration at night. Introducing the parameter g_{min} into the equation allowed us to estimate night flows. This minimal nocturnal stomatal conductance (g_{min}) was calculated as 0.00020 m s^{-1}. The highest stand canopy conductance of 0.0033 m s^{-1} and highest average conductance of 0.00107 m s^{-1} were calculated during the wet period.

3.3. Modeling sap flow and stomatal conductance: the classical approach

The classical approach, which applies an inverted P-M equation for calculating diurnal courses of stomatal conductance with subsequent regression analysis between calculated g_c and environmental variables (equations 7 and 8), also allowed for the estimation of stand water use in a diurnal resolution. Calculations of canopy conductance upon low D were subjected to an error typical for this method: when D was low, g_c unrealistically increased (Fig. 4e). The error in estimating long-term water use (i.e. during the wet period) was similar to the method of direct parameterization if only the periods of high D were considered. Correlation between measured and modeled sap flow was slightly less than it was for the model derived via direct parameterization (Table 2).

3.4. Comparison of proposed and classical approach and of different models for dependence of stomatal conductance on environmental factors

All models acceptably described diurnal courses of sap flow and stomatal conductance when the D was high, with R^2 of linear regression between measured and predicted values >0.94 and >0.87 for sap flow and stomatal conductance, respectively (Table 2). However, when low D was included, only the proposed approach was able to predict the sap flow with success. The classical approach yielded unrealistically high values of g_c (Fig. 4e) and there was no correlation between g_c and environmental factors (R_g and D). Therefore we were not able to model a sap flow when all data were used in a classical approach. A modified Lohammar equation incorporating parameter of minimal stomatal conductance (g_{min}) proved the most effective correlating with measured values, yielding highest R^2 and having the lowest AIC of all models. Absolute values of sap flow and stomatal conductance were generally more accurate when predicted by models incorporating parameter g_{min}, which were able to account for the effect of night sap flow.

3.5. Effect of soil water availability

Sap flow dropped by 95 % during the dry period (Fig. 3). The transient period showed a decrease in water use and lasted two months, from the end of April to the end of June. Daily sums of sap flow were successfully predicted in all wet, transient and dry seasons. Interpolation of SWP from 25 May to 12 June, after the single rain event during transient period, helped to model the decline in sap flow. Otherwise the model would overestimate

measured sap flow and in this period would reach up to the values predicted from the equation 5 (Fig. 3). The R^2 of a linear regression between measured and modeled sap flow was 0.93.

4. Discussion

4.1. Measured sap flow

Low values of daily sums of stand sap flow reflected both harsh tree line conditions at the altitude of roughly 2200 m a.s.l. (Fernández-Palacios and de Nicolás 1995) and low stand density. Stand transpiration in one studied forest stand was lower than average at 0.80 mm day^{-1} (with a maximum of 1.85 mm day^{-1}) in a lower situated stand of a *P. canariensis* (Luis et al. 2005). Stomatal conductance was also lower than in previous studies for lower altitudes (Wieser et al. 2002; Luis et al. 2005). A decrease in summer months of sap flow and stomatal conductance, which occurred during the studied period, was typical only for the higher altitudes, as summer drought at lower altitudes is often mitigated by a high frequency of clouds that do not occur at high altitudes in the summer (Gieger and Leuschner 2004; Luis et al. 2005; Wieser et al. 2006).

The estimated time lag of 1 hour between the diurnal course of global radiation and stem sap flow, on the lower end of a commonly used range of 0 – 4 hours (Martin et al. 1997; Čermák et al. 2007; Whitley et al. 2009; Ward et al. 2013) was typical for the tree species with reduced (more sparse) crowns and therefore smaller water storage capacity (Anfodillo et al. 1998). Response to changes in D during the day were faster than to R_g as once the pool of the easily accessible stored water is depleted, the hydraulic signals are transmitted throughout the plant at a very high speed (Malone 1993). A lag of sap flow compared to the potential evapotranspiration was also observed when the canopy was wet from rain. Such a lag time may reach up to two hours (Langensiepen et al. 2009). In this case, a simple P-M based model was not able distinguish between evaporation and transpiration and therefore could not accurately predict sap flow.

4.2. Comparison between direct parameterization and the classical approach

The classical approach for calculating g_c and transpiration (or sap flow) using the P-M equation consists of several steps. In the first step, g_c is calculated from eq. 7. The second step includes regression between R_g, D and g_c. Here, it is often necessary to introduce an

enveloping curve into the regression. Utilization of the inverted form of P-M equation, in combination with the exponential equation characterizing the dependence of g_c on D, causes an unrealistic increase of the g_c on low D (Fig. 4e). It happens because low sap flow is divided by low D, which brings large error into the calculation. To avoid this phenomenon, Ewers and Oren (2000) recommend excluding all data where D is lower than 600 Pa. This often affects considerable parts of a dataset and in our case we would reject 44 % of the data from the period of models comparison. The proposed approach using parameterization of the P-M equation with simultaneous derivation of all parameters, using an arc tangential relationship for D allowed us to predict g_c even on low D, and thus allowed us to predict sap flow for any time of day. Furthermore, the one-step calculation process proved to be the most consistent and resulted in the highest R^2 between observed and predicted sap flow and in lowest AIC of the model (Table 2).

These two approaches have, however, common limitations. First of them is that they are not able to distinguish between transpiration and evaporation. When the rain or dew occurs intercepted water is evaporated first from the needle surfaces before the transpiration follows. Evaporation consumes part of the radiation energy and increases the lag between potential evapotranspiration and sap flow. Second issue relates to the hysteresis pattern between sap flow and potential evapotranspiration (Oren et al. 2001; Matheny et al. 2014a; Matheny et al. 2014b). Trees store considerable amount of water in the needles, branches, stem and roots (Phillips et al. 2003; Warren et al. 2005; Čermák et al. 2007; Oliva Carrasco et al. 2015; Urban et al. 2015; Mirfenderesgi et al. 2016). Resistances to the xylem water transport make it easier to use some parts of the stored water for transpiration instead of withdrawing it directly from soil (Sack and Holbrook 2006). Therefore, gradient of water potential develops along the pathway of xylem water transport and time lag occurs between transpiration and sap flow. Water stored in the tree is refilled during the periods of low evapotranspiration demands. It brings further uncertainty into the modeling of sap flow from weather data. One solution would be to introduce tree water potential or water storage into the simulation, like in the resistance-capacitance circuit (Sperry et al. 1998; Steppe et al. 2006; Bonan et al. 2014) or porous media models (Bohrer et al. 2005; Chuang et al. 2006; Janott et al. 2011; Mirfenderesgi et al. 2016). These models are able to numerically solve for the water potential and they do not require it as a mandatory input variable because continuous measurement of water potential in conifers is a significant challenge and these data are often not available. Water potential can be estimated also indirectly, from the dendrometers readings (Perämäki et al. 2001) or from changes in a stem water storage measured by soil moisture sensors working on principle of time domain reflectometry (TDR)

(Irvine and Grace 1997) or frequency domain reflectometry (FDR) (Matheny et al. 2015; Carrasco et al. 2015). Even though these indirect approaches have been developed, such data are available only in a few studies. Therefore, with limited data availability, parameterizing of the P-M equation is still a viable option to calculate g_c and to model stand sap flow.

4.3. Different models for dependence of g_c on environmental variables

Stomatal conductance models relate stomatal aperture to global radiation and vapor pressure deficit. While R_g opens the stomata, D closes the stomata (Fig. 6). Strong correlation between g_s and D lead to the assumption that a functional relationship exists (Meinzer and Grantz 1990; Aphalo and Jarvis 1991; Addington et al. 2004). Both the Jarvis-Stewart model incorporating the added parameter g_{min} (eq. 8) and the modified Lohammar equation (eq. 4) acceptably described dependence of stomatal conductance on environmental variables with only negligible differences in R^2 of the models within a parameterized period.

The mechanism driving stomatal opening in the morning due to R_g led to an assumption about stomatal movements only during daytime conditions (Shimazaki et al. 2007). However, evidence of night sap flow response to ΔD suggests that large portions of water are lost through cuticular transpiration (Burghardt and Riederer 2003), stomatal closure is incomplete or that stomatal movements occur at night (Caird et al. 2007; Kavanagh et al. 2007; Zeppel et al. 2011). Caird et al. (2007) summarized a large body of evidence showing that g_s changes at night were based upon various driving factors, including D. We therefore incorporated the parameter g_{min} characterizing night stomatal conductance into the eq. 4. Inclusion of this parameter improved the correlation (Table 2). The parameter describing minimal stomatal conductance is not a new idea. Similar parameter was used for example in the Ball-Berry model. There is a difference between the g_{min} in our study and g_0 in the Ball-Berry model. While g_{min} describes a true minimal stomatal conductance, g_0 is a stomatal conductance at light compensation point of photosynthesis. Estimation of the g_{min} from the sap flow data is further complicated by the changes in water content in plant tissues. Therefore, the exact amount of water transpiration at night could not be accurately described from the sap flux measurements as we were unable to separate plant refilling from actual transpiration to the atmosphere (Wang et al. 2011). The hysteresis pattern observed in the diurnal sap flux response to changing D (Oren et al. 2001) indicated that refilling occurred. More complex models like FETCH2 (Mirfenderesgi et al. 2016) which recently

occurred would be needed to identify to what degree contributes aboveground tree water storage to the tree water uptake and transpiration.

4.4. Effect of soil moisture

Soil water content is the other driving mechanism of stomatal aperture (Granier and Loustau 1994; Zweifel et al. 2009; Brito et al. 2014). We defined a submodel describing the effect of actual soil water potential on plant sap flow. This modification allowed for modeling sap flow on a daily basis in wet, dry and transient periods of a season. However, a more thorough understanding of the soil water potential in rooting zones (or of the predawn tree water potential) and plant ecophysiological adaptation to imminent water stress is necessary. In our case study, sap flow did not scale with measured soil water potential in a short (two-week long) period after the rain event which occurred in the middle of the transient period, when measured soil water potential increased from -0.5 MPa to almost zero, while sap flow increased only slightly (Figs. 2, 3). Decoupling of the sap flow from measured soil water potential may occur for two reasons. The first may be that it is linked to the position of soil water sensors, which may not be able to describe true water availability for the tree root system (as rooting depth can easily reach 15 m, while the sensors were installed in 30 cm depth (Luis et al. 2005; Brito et al. 2015)). The second relates to a tree's ecophysiological adaptation to water stress (i.e. needle shedding, which was observed at the site (Brito et al. 2014), an accumulation of ABA, or embolism of xylem tracheids). Therefore, it is advisable to monitor predawn tree water potential, as an indicator of a tree water status, and to monitor longer-term tree adaptation to water stress.

5. Conclusions

1. Direct parameterization of the Penman-Monteith equation with an incorporated modified Lohammar model is a suitable approach to derive diurnal courses of stomatal conductance of the forest stand. Closer correlation between measured and calculated sap flow was found using the proposed approach by applying the direct parameterization than was observed using the classical calculation method.
2. Direct parameterization of the P-M equation allowed for calculation of canopy conductance upon low D and avoided unrealistic increases of computed g_c, typical for the classical approach of calculation. Furthermore, the direct parameterization approach does not require computing the enveloping curve and thus avoids subjective selection of the data by the user. Moreover, direct parameterization

allows for calculation of g_c and modeling sap flow to occur in one step. This makes it possible to quickly and automatically repeat the calculation, i.e. for different time periods.

3. The proposed modification of the Lohammar et al. (1980) equation successfully described dependence of canopy conductance on measured environmental variables (global radiation and vapor pressure deficit). Its modified form allowed for more precise descriptions of g_c, especially upon low D, then the commonly used three-parameter function. Including a parameter describing minimal stomatal aperture allowed for modeling of night sap flow.

Author Contribution Statement

JK contributed to the work by devising of the methodology, data analysis and work on the manuscript. MJ and PB performed the field work and contributed to the writing of the manuscript. JU contributed to the data analysis and writing of the manuscript.

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Conflict of Interest

The authors declare that they have no conflict of interest.

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716 Tables

717 Table 1. A summary of abbreviations and symbols used in the equations and throughout the
718 text.

a, b, c, d	parameters
AIC	Akaike's information criterion
c_p	specific heat of air [J m^{-3}]
D	vapor pressure deficit [Pa]
G	soil heat flux [W m^{-2}]
g_a	aerodynamic conductance [m s^{-1}]
g_c	canopy conductance [m s^{-1}]
g_{lim}	parameter related to maximal canopy conductance [m s^{-1}]
g_{min}	parameter of minimal canopy conductance [m s^{-1}]
g_s	stomatal conductance [m s^{-1}]
k	von Karman constant [-]
LAI	leaf area index [-]
P-M equation	Penman-Monteith equation
R_0	half light saturation [W m^{-2}]
R_g	global radiation [W m^{-2}]
R_n	net radiation [W m^{-2}]
SWP	soil water potential [MPa]
u	wind speed [m s^{-1}]
z	wind speed measurement height [m]
z_d	zero plane displacement [m]
z_o	canopy roughness [m]
γ	psychrometric constant [Pa K^{-1}]
Δ	slope of saturation water vapor pressure deficit [Pa K^{-1}]
λ	water heat capacity [J kg^{-1}]
ρ	density of dry air [kg m^{-3}]

719

720

721 Table 2. Index for determining of linear regression (R^2) between measured sap flow (or
722 canopy conductance) and those simulated by the model. Akaike's information criterion
723 (AIC) for various models. Simulated values of sap flow and stomatal conductance comes
724 from following models: the Jarvis-Stewart model (eq. 8), the modified Lohammar model
725 (eq. 4), the original Lohammar model (eq. 3) and values of sap flow and canopy
726 conductance calculated from an inverted P-M equation (eq. 7). Models incorporating
727 additional parameters of minimal stomatal conductance are labeled 'g_{min}'.

728

			D > 600 Pa		Entire period	
			R^2	AIC	R^2	AIC
Transpiration	Proposed model	Jarvis-Stewart gmin	0.955	-4503	0.934	-7128
		Jarvis-Stewart original	0.953	-4440	0.932	-7052
		Lohammar modified	0.954	-4447	0.933	-7058
		Lohammar modified gmin	0.956	-4515	0.935	-7139
		Lohammar original	0.949	-4417	0.929	-7022
		Lohammar original gmin	0.950	-4464	0.929	-7084
	Classical model	Lohammar modified	0.946	-4445	NA	NA
		Jarvis-Stewart gmin	0.940	-4412	NA	NA
Canopy conductance	Proposed model	Jarvis-Stewart gmin	0.907	-7080	0.000	
		Jarvis-Stewart original	0.907	-6999	0.000	
		Lohammar modified	0.908	-7005	0.000	
		Lohammar modified gmin	0.909	-7092	0.000	
		Lohammar original	0.904	-6985	0.000	
		Lohammar original gmin	0.903	-7058	0.000	
	Classical model	Lohammar modified	0.887	-7028	0.000	
		Jarvis-Stewart gmin	0.879	-7011	0.000	

729

730 **Figure captions**

Fig. 1. Diameter distribution of the pine trees at the research site, their number per ha (black bars) and the number and distribution of the sample trees used for sap flow measurements (grey bars).

Fig. 2. Daily means of global radiation (R_g), vapor pressure deficit (D, panel A), daily means of soil water potential (SWP) and daily sums of precipitation (panel B). Wet and dry periods are highlighted with a grey background. Dotted line on the panel B indicates values of SWP used to parametrize the model (9) after the rain event in the transient period.

Fig. 3. Daily sums of measured and modeled sap flow. Two models were used. One (equation 5, model without SWP) was parameterized on the period with the unlimited soil water availability (from 27 February to 5 April, 2008) and these parameters were used to simulate the sap flow during entire season. Second one (equation 9, model including SWP) included soil water potential into the simulation.

Fig. 4. Examples of diurnal curves of measured sap flow (black line), modeled values using the proposed approach (red line), and the classical approach (green line), (panels A, D). Typical diurnal courses of stomatal conductance (panel B, E) estimated using the classical approach from equation 7 (green line) and using the proposed approach (red line). Corresponding global radiation (R_g) and vapor pressure deficit (D) (panel C, F) for days with high (panels A, B, C) and low D (panels D, E, F).

Fig. 5. Measured and modeled values of sap flow using the proposed (A) and the classical approach (B) during the wet period (n = 955).

Fig. 6. Response of relative canopy conductance to global radiation (panel A) and canopy conductance to vapor pressure deficit (panel B) during the wet period estimated using the modified Lohammar equation.

Figure

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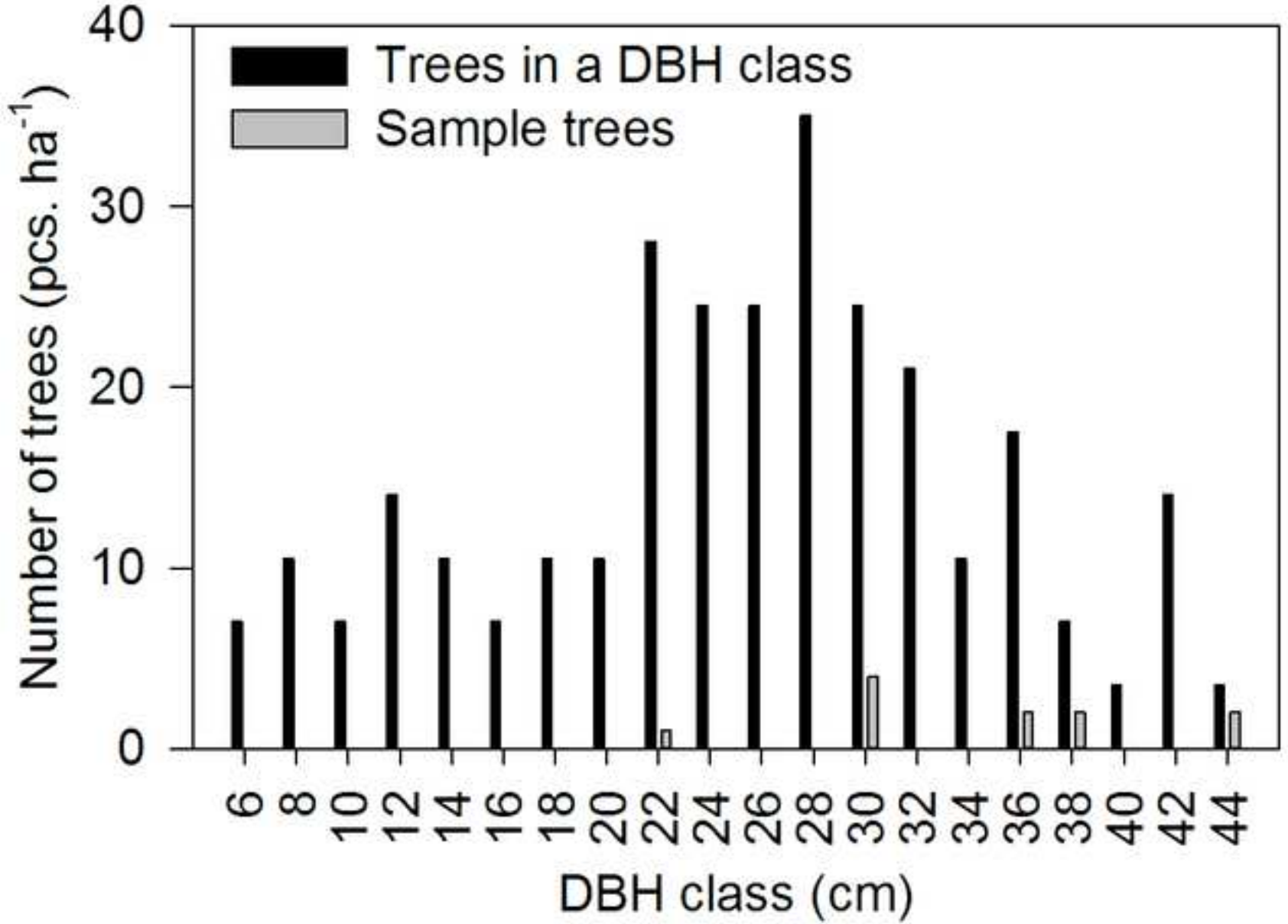

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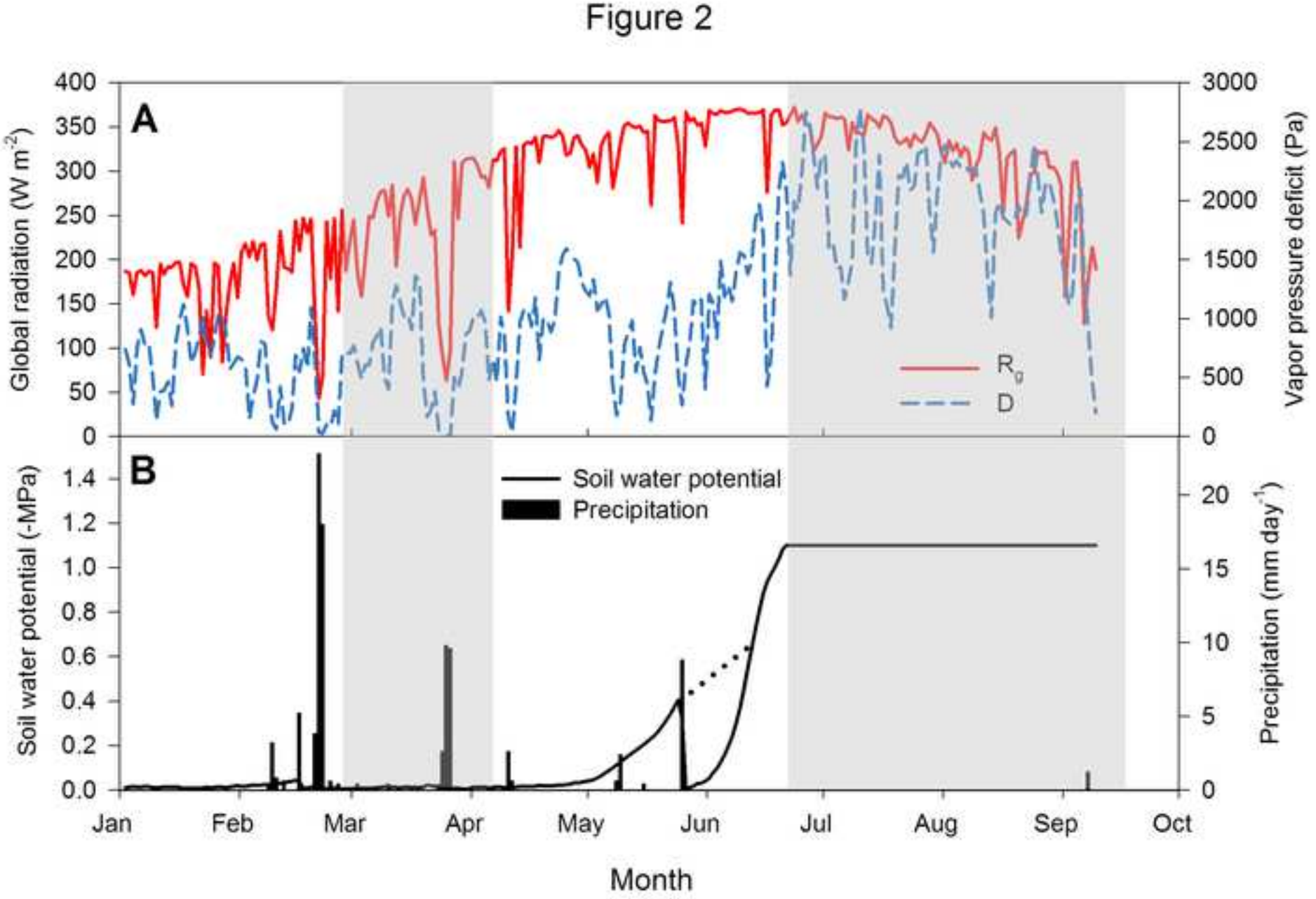

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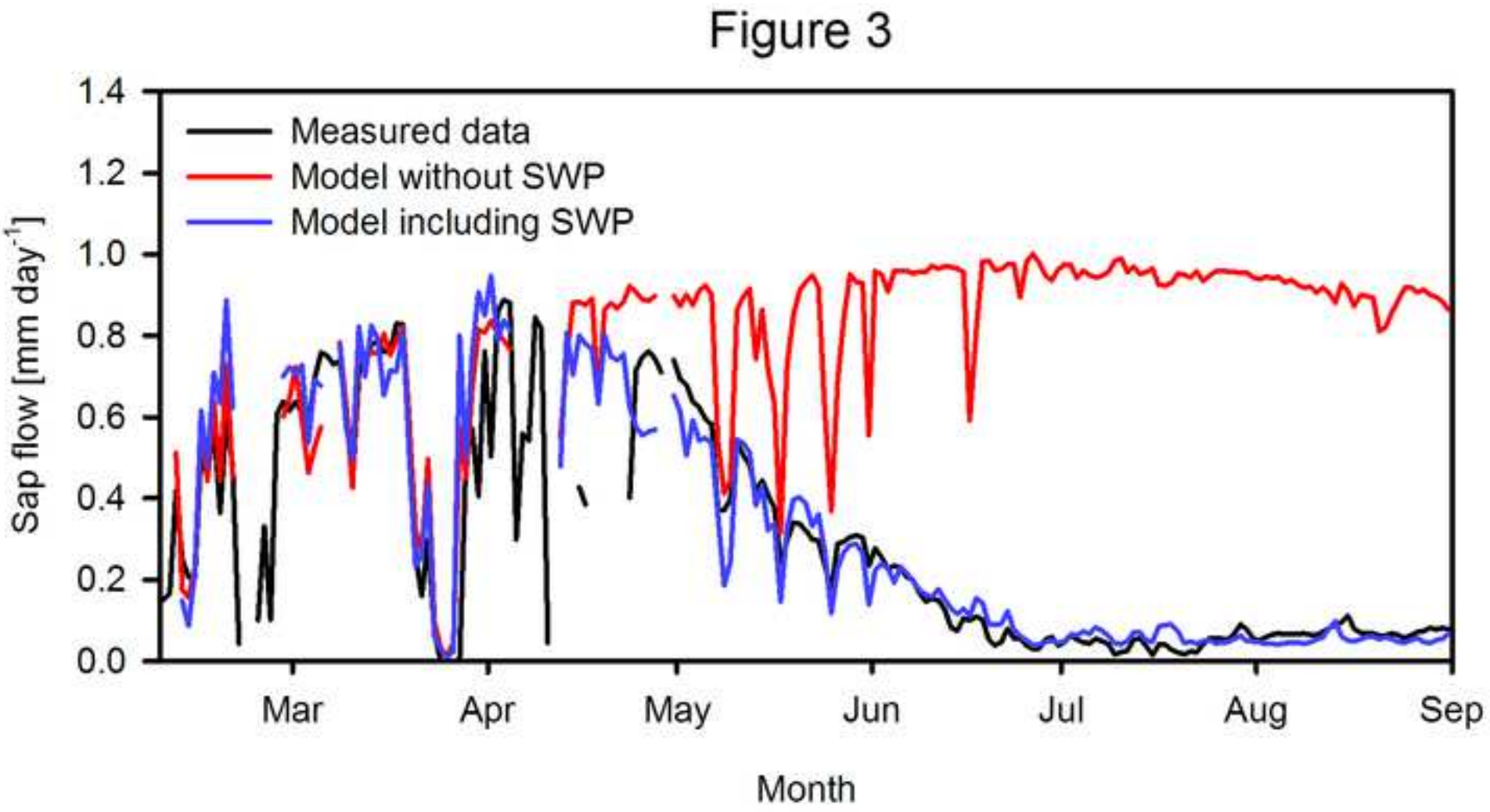

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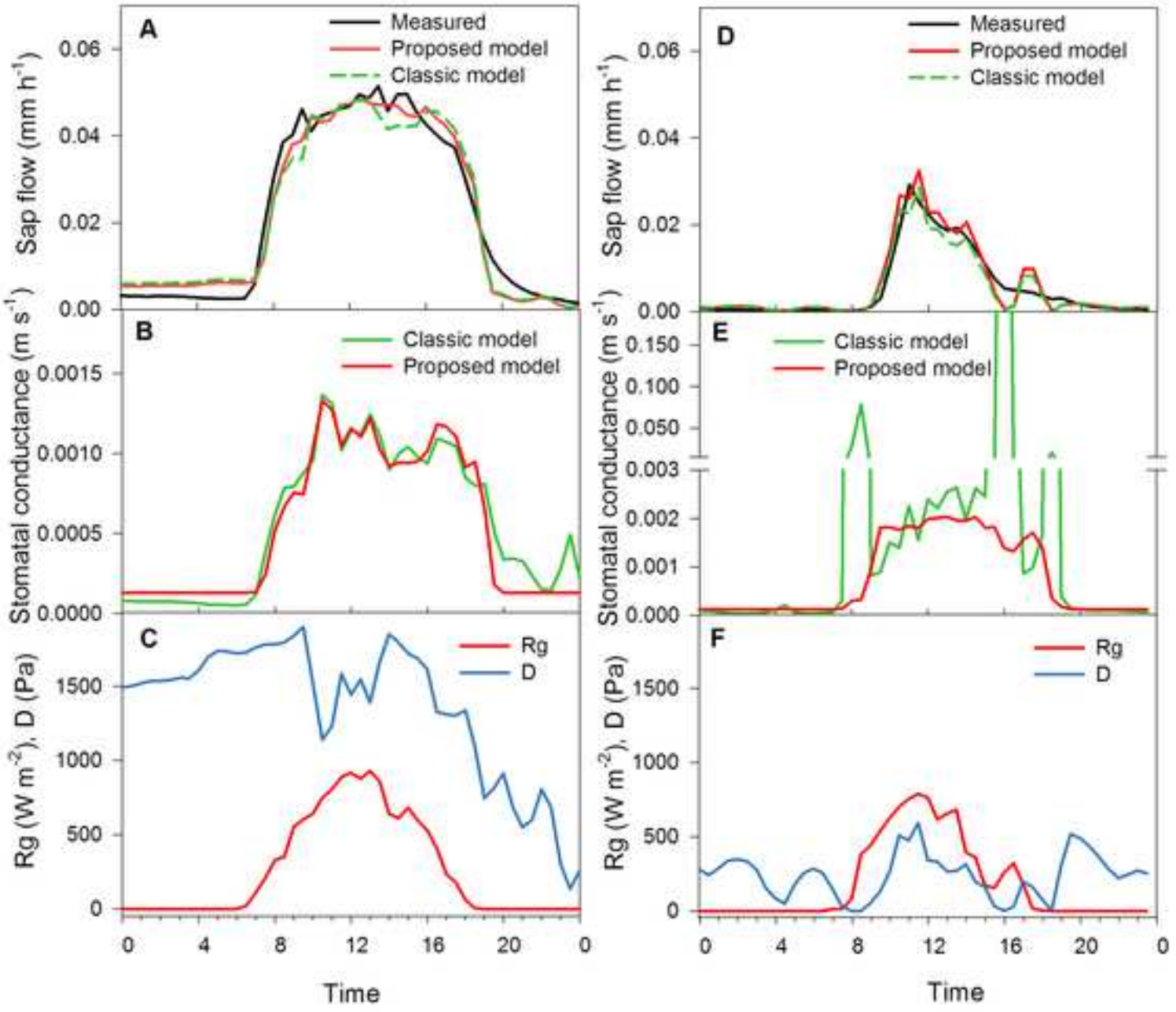

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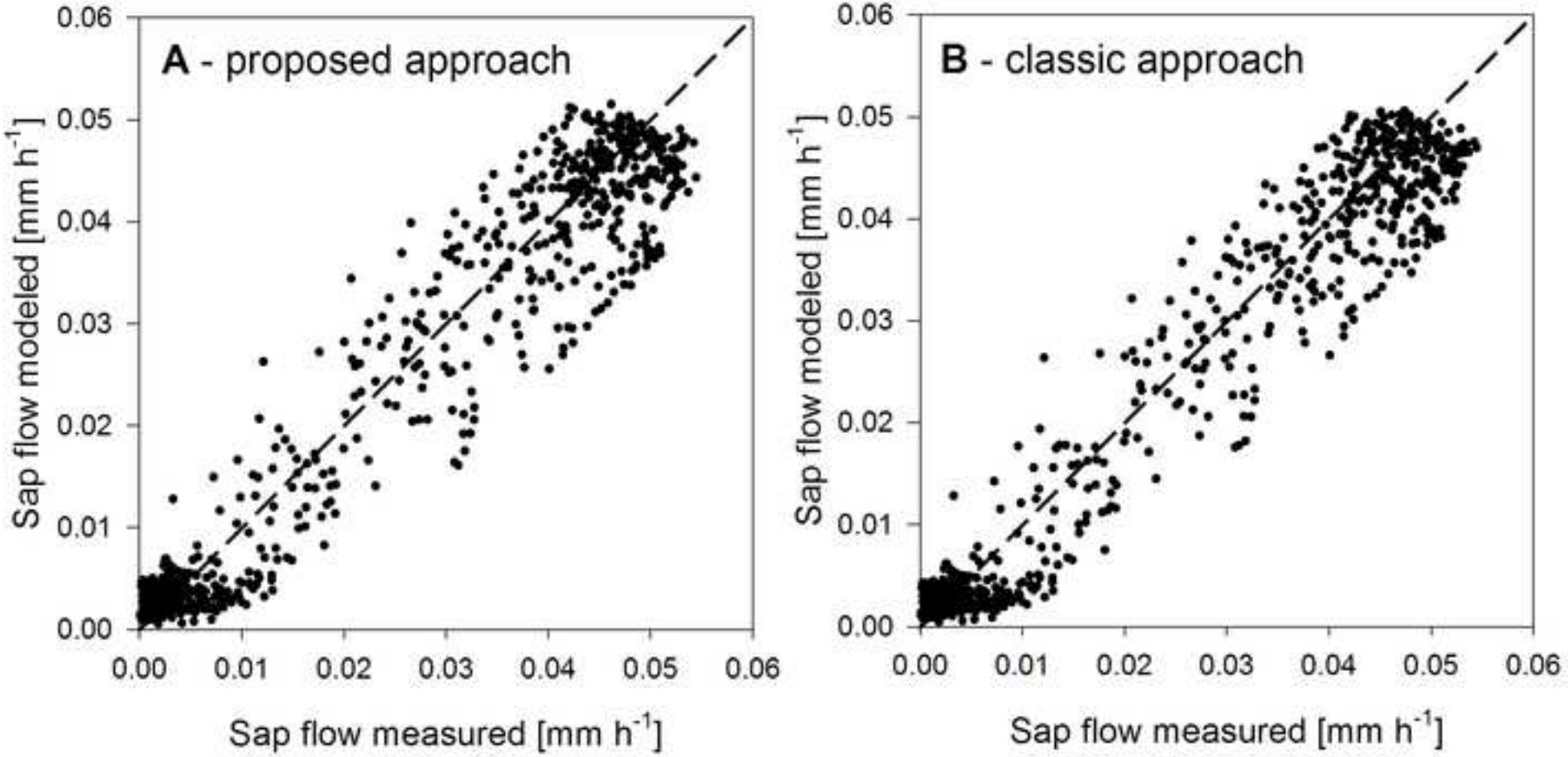

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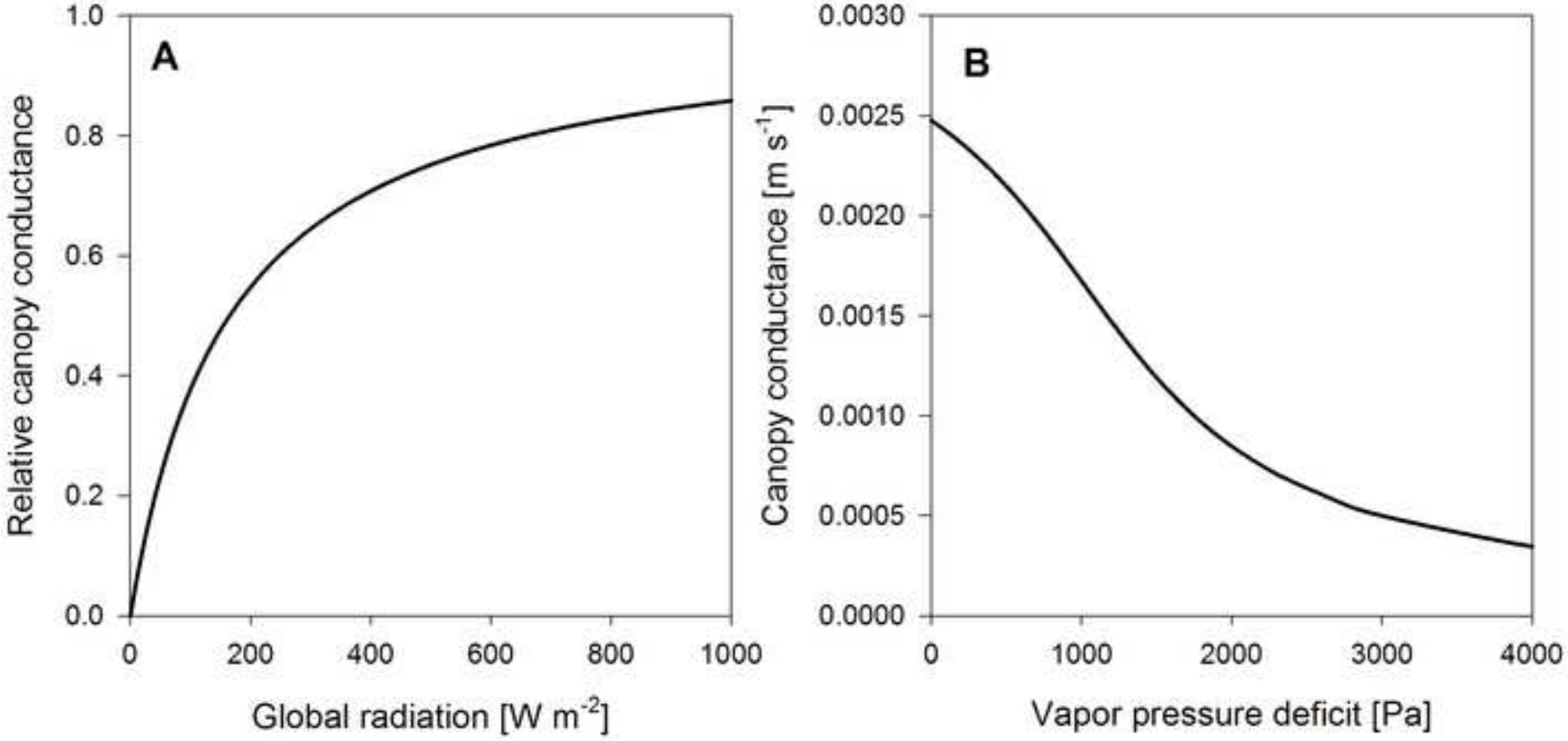

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